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THE RELATIVE ANNUAL GROWTH OF DIFFERENT PONDEROSA PINE MERISTEMS AND ITS IMPORTANCE IN EVALUATING CURRENT HEALTH SYMPTOMS

By

W. D. Bedard
Associate Entomologist

JMM
MLL
KAS
JLP
GRS
HLM
ASW
SMS
SCH
WSH
HSY
STC
PCJ
ESE

Forest Insect Laboratory
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The radial growth of trees has long been used as a standard measure of tree vigor and its response to changes in various environmental factors. However, the physiological concept of growth in woody plants considers four main meristematic regions which produce vertical elongation of the main axis, horizontal expansion through branching, secondary thickening, and leaf development. This places the main meristems in Pinus at the shoot tips, near the root tips, at the cambium, and at the bases of the needles. Thus a complete consideration of ponderosa pine growth should include: (1) Elongation of shoots, (2) elongation of roots, (3) secondary thickening by cambium, and (4) development in length, abundance and diameter of needles.

As far as could be ascertained, most of the work which has been done with tree growth deals with the activity of a single or at most two growing regions. Only one case[12] could be found in which the worker studied all four meristems at the same time. Leader elongation and cambial growth have been most frequently investigated, but only rarely have measurements of both of these growth activities been recorded simultaneously for the same individual.

In spite of this partial consideration of total growth, most investigators have been able to show statistically significant correlations between the type of growth measured and the environmental factor under consideration in their respective studies. Chalk,[3] Keen,[11] and Kienholz[12] showed such correlations between radial growth and precipitation; Evenden[4] and Graham[7] with radial growth and defoliation; Baldwin,[1] Korstian,[13] Hiley[8-9] and Cuncliffe, and Pearson[19] with leader growth, temperature, and precipitation; Kienholz[12] with leader growth and night air temperatures; and Reed[21] with root growth and precipitation.

This mass of evidence showing that the different meristems respond similarly to changes in the same environmental factor has led to the natural assumption that in general good and poor growing seasons are characterized by good and poor growth respectively in all meristems. No contradiction of this assumption could be found in the literature. However, that trees apparently do not show the same growth trends in all meristems in the same season was brought out strikingly in some small 10-tree reproduction plots near Bly, Oregon, in 1941, where leader growth, needle length, and fascicles per twig were counted preparatory to treatment with certain nutrients and injuries.

Evidence of Dissimilar Growth Trends

In establishing the nutrient plots, measurements and counts were made to determine leader growth per year for the past five years, needle length per year for the past four years, and the number of fascicles per twig per year for the last three years. It soon became evident in this work that growth trends were remarkably similar. There appeared to be few exceptions to the fact that greatest leader growth occurred in 1938 and least in 1936; longest needles in 1940 and shortest in 1939; and most abundant fascicles per twig in 1939.

When the counts and measurements were completed, an analysis demonstrated that nearly all trees showed the same general yearly growth trends in the same meristematic regions. This uniformity is shown in table 1, where yearly trends and the percent of trees showing the trend are tabulated.

Table 1: Growth trends by years in ponderosa pine reproduction and percentage of trees conforming to general trend.

(basis - 480 trees)

Type of growth	Year 1937	1938	1939	1940
Mean leader growth	increase	increase	decrease	decrease
% trees following trend	92.2	82.7	80.8	94.3
Mean needle length		decrease	decrease	increase
% trees following trend		46.6	100	100
Mean number fascicles per twig			most abundant fascicles	decrease
% trees following trend			100	100

After viewing table 1, there can be no doubt of the general nature of these trends. Mean needle length in 1938 is the only case in which there is an appreciable percentage of trees not conforming to the general trend. In this particular case, 38.4 percent of the non-conformist trees show neither an increase nor a decrease, and the remaining 15 percent made only fractional increases. For the most part, this condition also prevails among the trees which do not conform to the general trend in leader growth, but there are a few trees in this group which are more widely divergent in leader elongation. However, these data appear to be sufficiently conclusive without further analysis, to prove the validity of the yearly trends.

Although growth trends are uniform within individual meristems, it is also quite evident in table 1 that there is no similarity between the seasonal growth trends of the different meristematic regions. In 1939, for example, the number of fascicles per twig increased, whereas needle length and leader growth decreased; while in 1940 leader growth and fascicles per twig decreased and needle length increased.

Although no radial growth records will be available from these trees until the study is completed in 1943, it is interesting to compare the growth pattern for mature ponderosa pine in eastern Oregon with these other growth records. Keen's growth studies show a gradual improvement in ring growth from 1936 to 1939, followed by a drop in 1940. Table 2 gives a comparison of the eastern Oregon ring pattern with the growth records from this study.

Table 2: Needle and leader growth trends of ponderosa pine reproduction compared with radial growth trend of mature trees in eastern Oregon

Type of growth	Year				
	1937	1938	1939	1940	Probable 1941
Leader elongation	increase	increase	decrease	decrease	increase
Needle length		decrease	decrease	increase	increase
Fascicles per twig			increase	decrease	?
Radial growth mature trees	increase	increase	increase	decrease	increase

Table 2 indicates that none of the growing regions consistently shows the same or even similar growth trends. There appears to be an inverse relationship between needle length and fascicles per twig wherein increases in the one are accompanied by decreases in the other. There also appears to be a direct relationship between leader elongation and radial growth, with the exception of 1939.

Dissimilar growth trends are also shown by the graphs and tables in R. C. Hall's report[7] on some physiological factors of ponderosa pine growth. His records show dissimilar annual trends not only between meristematic regions, but also between vigorous and decadent trees. Assuming that the decadent trees would not follow normal growth trends, table 3 has been based only on the records for his vigorous trees.

Table 3: Annual growth trends in shoot and needle shown by Hall's vigorous trees

Type of growth	Year					
	1935	1936	1937	1938	1939	1940
Shoot elongation	increase	decrease	decrease[a]	decrease	increase	decrease
Needle length		decrease	decrease	increase	decrease	increase
Fascicles per twig				decrease	increase	decrease

[a] It is difficult to tell from the graph whether the 1937 twigs decreased in length as compared to the 1936 twigs, or whether they made an approximately equal growth.

By comparing table 3 with table 2, it is seen that growth trends in Hall's mature pines are not the same in all cases as those for reproduction. This could conceivably be an age or a climatic difference. The important point is, however, that dissimilar growth trends appear to be of normal occurrence in ponderosa pine development.

Theoretical Explanation

The literature was searched to find an explanation for the apparent fact that the different meristematic regions of individual trees do not follow the same growth trends. Since there apparently has been no previous expression of this thought, it is obvious that no direct explanation was found. However, literature dealing with growth stimuli in individual meristematic regions was found to be rather abundant. Most of this work deals with cambial development, a lesser amount with shoot elongation, a rather small number with needle growth, and only two with root elongation. Growth in each of these regions will be discussed in the order named.

Concerning cambial development, there appears to be general agreement that first growth in the spring is closely correlated with temperature, while summer wood growth is dependent on available moisture. Lodewick[16] found that precipitation was important in controlling summer wood growth but that spring wood was not as greatly influenced by it. Chalk[3] reported spring wood volume correlated with May-June mean temperature and summer wood volume with June-July-August rainfall.

This dependence of early cambial growth on temperature causes wide variations in the time of its inception both in different trees of the same species and within individual trees, because of differences in location and exposure. Pearson[20] found first growth in ponderosa pine to vary for different localities. Romell[22] reported that in Scotch pine, cambial growth began a few days before height growth one year and from two to three weeks later the following year. Brown[2] and Lodewick[15] concluded that the seasonal inception of cambial activity varied for different trees of the same species. Thus, differences in time of growth inception and degree of stimulation during the growth period cause radial growth to be irregular and often eccentric as reported by Brown[2] Chalk[3] and Graham.[5]

Greatest shoot growth is made at night during spring and early summer. Hence shoot elongation is influenced most by night air temperatures and very little by precipitation because of an abundant supply of soil moisture during most of the growth period. Kienholz[12] showed a high degree of correlation between night air temperatures and leader growth in red, white, and pitch pines, spruce, and fir. There also appears to be a relatively short growth period by shoots as shown by Kienholz[12] and Pearson.[19] Leader growth begins about the same time as cambial activity, but is completed before any great influence can be felt from summer precipitation. It would appear, however, that growth trends in shoot and cambial growth are more nearly comparable than between any other meristems. This is indicated by the data in table 2.

Needle growth appears to be on a decidedly individualistic basis. First growth may occur before, during or after the beginning of growth in any other meristem. Normally, however, it appears to follow the first surge of the other three growing regions. Needle growth continues longer than shoot growth, but not as long as cambial and root growth. However, Kraus,[14] Haasis,[6] and Lodewick[17] found needles elongating during the second year. On the other hand, Meissner,[18] Honda,[10] and Kienholz[12] found no second-year growth. No records could be found concerning the factors influencing needle growth.

Root growth is continuous throughout the year except for short periods of extremely cold winter temperatures. However, Reed[21] found that although root elongation in loblolly and short leaf pines proceeded for twelve months, as contrasted with a five-month period when shoots grew, approximately four fifths of the root growth occurred during the period of shoot growth. Thus, temperature, which bears a direct relation to growth in other meristematic regions, has little effect on roots except during low temperature conditions of winter months. On the other hand, Stevens[23] reports that a deficiency in soil moisture seems to limit root growth at times during the summer months at the precise time when shoots of the same trees may be growing very rapidly.

In summation of these references, there appears to be normally a certain interrelation between the different growing regions of the tree, as far as inception and termination of growth is concerned. There appears to be first a great surge of growth in cambium, leader, and roots in early spring when air temperatures are rising rapidly. This rapid surge in growth appears to be due not only to favorable temperature and moisture conditions, but also to large amounts of stored food which become available to growing tissues in the presence of abundant moisture in the wood. After this first surge of growth in these three meristems, the needles reach their maximum growth rate, followed by a second peak in cambial growth. After nearly all growth is completed and the full complement of needles is functioning, the roots reach their second maximum of elongation.

Thus, although each of these four meristematic regions respond nearly similarly to the same environmental factors, their responses vary greatly in degree, and most significant of all is the fact that the period of greatest influence may occur at different times. When two or more meristems are growing simultaneously, there must be a constant and probably severe competition for growth materials since each growing region draws water, elaborated foods, and in some cases mineral nutrients to itself. As one growing region increases in activity, the attraction it exerts on available growth materials becomes greater. This decreases the supply available to some other growing region, which may gradually cease its activities through lack of materials. Although there must be an internal balance between the metabolic activities of the different meristems, it is quite conceivable that a varying deficiency or abundance in one environmental factor would have a greater effect on the growth of some meristems than on others and would logically produce differences in growth trends.

Implication in Health Symptom Evaluation

The significance of these dissimilar growth trends in the work of evaluating current tree health symptoms is readily apparent. Extremely short needles may appear during seasons of excellent growth in other meristems--a situation which actually occurred in 1939. Conversely, there may be a decided improvement in needle length when growth in other meristems is declining, as in 1940. On the other hand, the entire crown may indicate excellent health, but if there has been no comparable growth in roots, a rapid crown deterioration must follow during subsequent seasons until the balance has been re-attained. It would appear, therefore, that many variations are possible, all of which differ in importance. Some are merely temporary and of no great significance, while others are more permanent and may be quite serious or even fatal.

Obviously, there must be a recognition and understanding of all of these general trends before one can segregate general characters from those which specifically indicate a high susceptibility to beetle attack. Thus, a knowledge of causes and their effects is the most feasible means of reaching a rapid solution to the problem of symptom evaluation.

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